XI. — *A Critical Examination of Mohl's Views of the General Structure of the Pollen Granule.* By Arthur Hill Hassall, Esq., M.R.C.S.L., Corresponding Member of the Dublin Natural History Society.

Mohl considers the external membrane of the pollen granule to be the secreting organ of the oily liquid found upon all pollen, but more abundantly upon such as is either cellular or spinous, and that it is this liquid which determines the colour as well as the viscosity of the pollen.

In the remarks I have already published upon the pollen granule*, I have suggested the probability that this viscid fluid, which differs so much from the fovilla in appearance, is derived from the cell in which the pollen is originally developed; and this suggestion appears to gather some degree of confirmation from the fact of its being met with in greater quantity upon pollen which has just escaped from the anther.

This external membrane Mohl states to vary considerably in intimate structure according to the plants in which it is examined, being either cellular or granular, and but rarely, if ever, perfectly homogeneous. "The cellular structure," he observes, "without being rare, occurs but in a small number of plants. It is met with as frequently among Monocotyledons as among Dicotyledons. It is not a character of a family; on the contrary, this structure is observed in genera of the same family, or in species of a genus, while allied plants present another." My opinion upon this point is, that it most frequently, if not invariably, is to be relied on as affording a character of at least generic importance, and that it is not uncommonly of higher value, running through several contiguous genera. The cellules are more or less regularly six- or seven-sided, and of various sizes. The network formed by their union has been mistaken by some observers for the ramifications of vessels in the external membrane of the pollen granule, "an error similar to that which had place relative to the epidermis of leaves." "In all cases where the external membrane is cellular," Mohl goes on to remark, "I have found the surface of the granule smooth and destitute of spines." "This result is in truth altogether opposed to that M. Brongniart announces, who believes to have found in the centre of each cell an excretory conduit under the form either of a hair or a spine; for example, in *Mirabilis Jalapa, Ipomœa purpurea*; but my observations have informed me, that all the species of pollen described by M. Brongniart as cellular and spi-

* See Annals and Magazine of Natural History for Oct. last, vol. viii. p. 92.

nous are not really at all cellular, and that the oil which is found in the cells does not escape by visible apertures, but transudes through the walls of the cells."

In making the above statements Dr. Mohl and M. Brongniart are both in part in error. Mohl errs in asserting, in opposition to M. Brongniart, that the kinds of pollen which are spinous are not at the same time cellular. In the paper already referred to, I have declared that the majority, if not all (and I am inclined to think that all are so), of pollen granules which are furnished with spines have a cellular extine; and that on *each* cell, and probably formed by it, either a spine is situated, or where this is absent, its walls are perforated by an aperture, which aperture is intended for the passage of the pollen tubes. On the other hand, M. Brongniart is doubtless at fault in the belief that he has found, in each cell of the reticulated external membrane, an excretory duct under the form either of a hair, spine, or aperture. In the pollen of *Lilium*, *Pancratium*, and many other plants whose external membrane is most manifestly cellular, neither apertures nor any other visible outlets, save the longitudinal furrow for the pollen tube, are discernible; in these cases, therefore, the oily matter must escape (if it be secreted by the extine) by exudation from the general surface of the membrane, and not through apparent openings. The spines themselves are for the most part open at their extremities, and may, where they are present, perform the office attributed to them by M. Brongniart. M. Brongniart refers to the pollen of *Mirabilis Jalapa* in support of his views. It is very doubtful whether the extine of this be cellular or not, and although it is indeed perforated with numerous apertures, these all undoubtedly are designed to permit the escape of the pollen tubes.

That the external membrane of most pollen which is hispid is really cellular, any one may satisfy himself by a careful examination of the pollen of *Ipomæa purpurea*, *Cynara Scolymus*, *Pavonia præmorsa*, *Hibiscus annuus*, &c.

Mohl thus speaks of the granular appearance sometimes presented by the extine, and as his observations on this point are highly interesting, I need make no apology for introducing them at length in his own words. "In many cases the cellules of the external membrane become contracted to such a point, that one knows not whether we ought still to give them the name of cells, or whether the membrane is only made up of very large grains. In these instances one might still admit that the granular aspect of the membrane arose from the fact of its being composed of extremely small cells, although our means of observation permitted us not to recognise these

grains for cells." This idea of Mohl's is supported principally by reference to the fact, that in some pollen—for example, in that of *Pitcairnia latifolia*—manifest transitions from one of these formations to the other, that is, from the cellular to the granular, may be detected. This explanation is probably the right one.

"A question difficult to resolve is, to know if one might still admit the existence of very small cells, when the external membrane appears to be no more formed of large grains, but presents a smooth surface with very little points (or spots), cases without comparison more frequent than that of the true cellular formation of the external membrane. The solution of this question is allied to the clearing up of some points of vegetable anatomy still very obscure, and which have not sufficiently fixed the attention; I mean to the exact knowledge of the structure of those cryptogamous plants among which first begin to appear certain rudiments of cells in the gelatinous mass which forms them, under the form of little grains, for example, *Ulva*, *Palmella*, *Hydrurus*, *Batrachiospermum*, *Myurus*, &c., and afterwards to the inquiry of the manner in which the cells are united to each other in plants of higher development."

"A detailed examination of these points," continues Mohl, "would delay us too long; we pass on then to observe, that the gelatinous material, which forms by far the greater part of the bulk of these Cryptogams, corresponds to an element reduced almost to nothing in more elevated plants, which is found between the cells and produces their reciprocal union, but whose anatomical examination is only possible in a small number of vascular plants, and that the little scattered grains ought to be considered as the analogues and first rudiments of cells. Such is likewise, according to me, the organic constitution of the [granular or] dotted external membrane; it is then formed of two elements: 1st, of small grains of a cellular nature; 2nd, of a uniform material of a gelatinous nature which unites these grains into a membrane. Not only is this view supported by the accordance which this granular membrane offers with the constitution of the plants of which I have spoken, but there are direct observations which are in its favour. One circumstance which speaks for the analogy of the grains with the cells is, that in the grains of pollen whose external membrane is of a granular nature, as well as in those which are provided with a membrane distinctly cellular, the oily substance, coloured, is formed and preserved in this external membrane. Another fact, which is still further favourable to this view, is the series of modifications by which

an almost insensible transition is formed, from manifest angular cells even to the grains themselves." Here I would observe that Mohl has already recorded his belief that the large granules in one plant are really cells, for example, in *Pitcairnia latifolia*. "We now come to facts calculated to produce the admission, that the external membrane is not only made up of grains resembling each other, but that there is formed in it moreover a substance half membranous, half gelatinous. There are cases, where these grains, when the pollen is extended by the imbibition of water, do not touch each other; but instead of being pressed one against the other, as in most pollen, they appear scattered upon a membrane smooth and uniform, for example, in *Plumbago cærulea*, *Jatropha urens*, &c. It happens also sometimes, that in causing the grain of pollen to roll in a drop of water, between two small plates of glass, that some portion of the external membrane is detached from the granule which it surrounds, and that this part presents the appearance of a uniform (homogeneous) and colourless membrane. Moreover, as we shall show further on, the external membrane of most pollen presents regular plaits, which are effaced by the extension of the grain in water. Upon the part which in the dry pollen is concealed by the folds, the grains are altogether wanting, or form groups scattered at great intervals, so that the grains are placed upon a uniform membrane, and are separated one from the other by the extension of that membrane. It is not an uncommon circumstance to find the external membrane, at the situations where it covers the papilliform processes of the internal membrane, deprived of grains and completely uniform. Whether even these proofs shall be deemed sufficient, as I now think them to be, to establish the analogy of structure and of functions between the well-formed cells and these grains, it is nevertheless, at all times, but an analogy, and we have no right to regard them as cellular tissue itself, but only as the rudiments of cells. The granular disposition of the external membrane is by much the most frequent. As we have met with gradual transitions from the membrane plainly cellular to the granular and dotted membrane, in the same manner, this itself does not always present itself equally well-formed, and we find in many species grains becoming smaller and smaller, until the membrane becomes almost completely smooth and homogeneous, and thus presents a striking resemblance with the membrane of ordinary vegetable cells. This is the case, for example, in *Allium fistulosum*, *Chamærops humilis*, *Araucaria imbricata*, *Rumex scutatus*, *Morina persica*, in the *Boraginaceæ*, *Chenopodeæ*, *Myrtaceæ*, *Graminaceæ*, in *Rivina brasiliensis*, &c.

"In these plants the granular formation tends so to disappear, that the external membrane presents only obscure little dots, which have scarcely any resemblance with cells. Lastly, in other kinds of pollen the grains disappear entirely, and the membrane is almost completely smooth and uniform. Nevertheless, in most cases, when the pollen is observed in water, we are able still to recognise, with the assistance of a good instrument, a very fine punctuation and a light yellow colour of the membrane, from which circumstance it is very probable that the external membrane is never perfectly homogeneous, but contains always grains, however little distinct they may be. All that has now been set forth appears to prove that the *comparison of the external membrane of the pollen granule with a vegetable cell is altogether inexact, and that it ought to be regarded as an organ composed of cells, or of the rudiments of cells, and of a homogeneous element which unites them; and for this reason also, to compare it, not with the simple membrane of a vegetable cell, but with compound membranes, for example, with the membranes of the ovule.*"

I have stated elsewhere*, that the granular appearance sometimes presented by the external membrane of the pollen granule frequently arises from the circumstance of the active "molecular bodies" being visible through the transparent coverings of the granule, so conveying to the outer one a granular or dotted aspect. That this appearance is often, if not always, deceptive, I am still of opinion, for additional reasons. Mohl states, that upon the part which in the dry pollen is concealed by the fold, the grains sometimes form groups scattered at great intervals. Now the radiating bands, of generally a lighter colour than the proper external envelope of the pollen granule, which supply the place of the furrows on the immersion of the pollen in water, are produced by the protrusion of the *internal membrane* through the fissures in the extine placed at the bottom of the furrows, and provided for the free egress of the pollen tubes; and this membrane is admitted by Mohl, and all observers, to be a simple structure. This, although a negative objection, is still a strong one. Again, in another place Mohl observes, that in some cases it happens that a portion of the extine is detached from the internal membrane, and that this part presents the appearance of a uniform and colourless membrane: this also goes to prove that the external membrane is, in some cases at least, simple. I am, however, still willing to admit, that in some few instances the external membrane may really present a granular texture, and then

* In *loc. cit.*

Mohl's explanation of the nature of these granules and of the constitution of this membrane appears to me to be satisfactory and philosophical; but I am far from going to such an extent as to suppose that the extine is never a simple organ, analogous to a primitive vegetable cell; on the contrary, I believe it to be most commonly simple.

Mohl considers that the spines and papilliform eminences which cover the external membrane of many forms of pollen take their origin in a special development of one of the grains of the external pollenical membrane, and that they constitute a partial development of the granular membrane into the cellular. This supposition of Mohl's is decidedly erroneous. I have already declared that most, if not all, kinds of spinous pollen have a cellular external membrane, and that the spines themselves owe their existence to an extraordinary development of the outer surface of each cell, in the same way as the hairs of the epidermis of plants are produced. Concerning the nature of the papilliform projections, Mohl appears to me to be far astray. They are not occasioned by any prolongation of the external membrane, which has nothing whatever to do with their formation; they are produced by the bulging out of the intine when there are but two membranes, or of the intextine when there are more than two, through either fissures or apertures in the extine.

It has been observed before, that on the immersion of those forms of pollen which exhibit furrows upon their surface in water, or any other fluid of the same consistence, that the plaits disappear, and that bands of a lighter colour than the rest of the surface of the granule occupy the position of the plaits, the appearance of these being accompanied by a remarkable change in the shape of the granule in all those cases where it is of an elongated form; this change arising from the approximation of the extremities of the granule, occasioned by the imbibition of the surrounding fluid by endosmosis. These furrows vary considerably in number, from one to upwards of twenty, a single furrow, for the most part, being characteristic of a Monocotyledon and three of a Dicotyledon; and the bands which supply their place subsequently are invariably disposed in a radiating manner, are narrow at their commencement near the centre of the figure, and widen gradually as they approach the circumference. These light bands Mohl regards as spaces of the extine, thinner than the rest of the membrane, and consequently more transparent. He thus speaks of them:—"In all cases where the bands are dotted, there is no doubt that the external membrane forms a vesicle completely closed; but upon pollen whose bands pre-

sent a smooth membrane, an opposite result is almost always encountered when one examines them when fresh. The membrane of the bands is then so delicate that it is torn either merely by the extension which the grain of pollen undergoes in water, or by the separation of the external membrane in such a manner that the bands appear to be true solutions of the continuity of the external membrane, in which cases the internal membrane is denuded by the swelling of the grain in water. It was not long after this observation that the examination of pollen a long time dry set right my ideas upon this point; in fine, I have always been able to observe the external membrane in the folds, in pollen in a dry state. It appears then, that the external membrane acquires by drying a very great hardness, while in the fresh pollen the concealed part of this membrane in the folds appears to possess a consistence rather gelatinous than membranous, from which it follows, that not being able to bear any great extension, it tears and presents itself in this state to the observer." In another place Mohl remarks, "but the portion which was concealed in the fold always presents a structure different from the rest of the membrane, although it is an immediate continuation of it."

My own observations do not permit me for a moment to doubt that these bands are formed, as already mentioned, by the protrusion of the internal membrane through fissures in the external, which are true and natural solutions of continuity in that membrane. This view of their nature is supported by several facts, which, when taken together, may safely be considered as conclusive: 1st, these bands differ from the external membrane in being of a lighter colour; 2nd, they are separated from that membrane by well-marked and raised lines of demarcation; 3rd, in cases where the external membrane exhibits a cellular formation, this structure cannot be traced on to the bands, although Mohl asserts that in some instances it may be thus traced; 4th, the pollen tubes are a growth or direct continuation of the bands; 5th, the bands are in some cases covered by a valvular piece of membrane, which is really a portion of the outer membrane, and when this is removed the bands themselves become visible, presenting their usual appearance; 6th, the existence of fissures in the external membrane may be demonstrated. In the dry pollen a fissure lies concealed at the bottom of each of the furrows, which generally run lengthways from one extremity of the granule to the other. In this state its edges are inverted and in *contact*, so as to prevent the egress of the pollen tubes; but as soon as the pollen comes to be immersed in water or the stigmatic se-

cretion, it undergoes, as already mentioned, a singular change of form, the cause of which has been explained: nor is this change of form without purpose, for in it may be traced a very beautiful little example of contrivance, it being designed to facilitate the escape of the pollen tubes from the external covering of the granule, which, in its dry state, for the sake of security, imprisons them. The granule swells and contracts in its long axis, the furrows become obliterated, and the margins separated as an inevitable consequence of this approximation of the extremities of the granule, and a space is left between them, through which there is a free and unimpeded passage for the pollen tubes hitherto incarcerated for wise purposes, but now that the fitting time has arrived, liberated by the above simple but most effectual means.

With reference to the apertures found in the external membrane of numerous forms of pollen, which are either scattered in no definite manner over the general surface of the granules or are placed at certain angles of its extent, Mohl asks the following question:—"These pores,—are they really apertures, or are they anything more than a very great thinness of the external membrane, in certain points like the pores of cellular tissue? It is a question which I cannot resolve for the smallest of these pores; but in pollen, in which they acquire a more considerable size, I have been able to convince myself in a manner the most evident, by the separation of the external membrane, that these pores are not true openings, but are closed by a fine membrane."

This last statement I also consider to be untenable for the same reasons given for regarding the bands as true solutions of the continuity of the external membrane.

From the brief exposition which has now been given of Mohl's views of the structure of the external covering of pollen granule, it is manifest that he regards it as being *in all cases* a compound organ, and as forming a shut sac, being thinner in the situations of the bands and pores; opinions in which I cannot concur.

Mohl thus concludes his account of the external membrane:—"After the description given above of the cells, spines and grains of the external membrane, it is clear that these parts ought to be considered as the secreting organs and reservoirs of the viscid oil; from which it follows, that the secretion of this oil ought not to be attributed to the papilliform eminences covered by a prolongation of the external membrane destitute of grains, and which are only found in some forms of pollen, and that even when the membrane, being furnished with fine grains which cover the large papillary projections

of the *Onagrariæ* and *Proteaceæ*, takes part in this formation, it is only in a much less degree than the rest of the surface. I cannot therefore adopt the opinion of Mr. Robert Brown, who especially attributes to these papillæ the secretion of the viscous matter." I have shown that the external membrane does not enter into the structure of the papillæ, and therefore in no instance can they have any participation in the formation of the fluid referred to.

Mohl considers the internal membrane of the pollen granule to be a simple homogeneous structure, and assigns to it the office of secreting the fovilla, a function which it appears to me to be very doubtful that it really performs; for in watching the progress of the formation of the pollen, the existence of the fovilla will be detected before any trace of the presence of the enveloping membrane can be discovered. This membrane, unlike perhaps all others which enter in the construction of the pollen granule, forms a closed cell, and is analogous to a primitive vegetable cell.

The interesting and remarkable facility, first discovered by M. Dutrochet, possessed by all organic membranes, whether vegetable or animal, of absorbing water or any other fluid of a less dense nature than that contained within their cavities, is thought, by M. Dutrochet, to pertain in a very high degree to the internal membrane of the pollen granule. For my own part, I do not see how a similar facility can be denied the external and other membranes of the pollen granule, since the water absorbed by the internal must necessarily, in many cases, pass through the outer before arriving at the inner membrane, and since it is the presence of the fluid which gets between the membranes which assists powerfully in causing the expulsion of the pollen tubes, from the pressure which it produces on the internal membrane.

This absorption of fluid by the investing membranes of the pollen granule sometimes takes place with such force as to occasion the rupture of the internal membrane, and according to Mohl, of that also of the thin part of the external; for it is only in this way, if Mohl's views are correct, that the pollen tubes can emerge. In the dilute mineral acids this effect is very frequently produced, but not always; and when it does occur, the effusion and coagulation of a portion of the fovilla, which often assumes a cylindrical and tortuous form, is the result, and with respect to which Mohl gives the following caution:—"We ought not to confound this mass, as has been done by M. Meyen, with the internal membrane issuing in the form of a tube; the first is distinguished easily from the second by its irregular form. M. Fritzsche, falling into

the same error as M. Meyen, considers the action by which the acids occasion the pollen to burst and coagulate its contents as of the same nature as the action of water and the stigmatic secretion. M. Fritzsche does in truth distinguish between natural tubes and tubes produced artificially, and he refers to the last those which are formed in consequence of immersion in an acid, while he ranges under the first denomination those which are developed from the effect of moisture upon the stigma or upon the corolla when the grains of pollen fall there; but he attributes to them the same origin, in admitting that they are formed by the mucilaginous part of the fovilla, and that they issue by breaking through the internal membrane of the pollen granule. This certainly occurs in the formation of the tubes which he considers as produced artificially; but the natural tubes differ absolutely, in that they are immediate prolongations of the internal membrane, of which we may be convinced by detaching the external membrane. It is indeed true, as M. Fritzsche says, that these tubes pierce a membrane; but that membrane is not the internal, it is the external, which is not pierced with holes, as M. Fritzsche thinks he has observed, but, as I have above explained, lines the pores, sometimes under the form of a fine membrane, sometimes under that of an operculum."

These observations of Mohl are in part only correct. Fritzsche is doubtless in error in supposing that the pollen tube which is to convey the fovilla through the tissue of the stigma and style to the ovary, is formed by the coagulation and hardening of the surface of the cylindrical mass, and not, as it really is, by the continued growth of a portion of the internal membrane; but I cannot see that there is any essential difference between the mode of action of water or the stigmatic secretion in the production of pollen tubes, and that of any of the dilute mineral acids; the only difference which I can detect being, that the latter, from the force with which it causes the principle of endosmosis to operate, most frequently, but not invariably, occasions the rupture of the internal membrane and consequent effusion of its contents, a thing which the former does sometimes, but much less frequently. If *dilute* sulphuric acid be used to the pollen of *Scabiosa caucasica*, true pollen tubes will be emitted covered by the internal membrane, and differing in no way from those the result of natural processes. The difference is not in the *modus operandi*, but in the effects of the agents.

If my views of the nature of the folds and apertures be correct, no membrane is ruptured, not even the extine, as stated by Mohl, save in the comparatively rare cases in which the

external membrane does really form a closed cell. The appearance of a thin film stretching across the apertures may be sometimes produced by the watery medium in which they are generally viewed.

The following remarks of Mohl are somewhat opposed to the opinion expressed by him, that the internal membrane should always be regarded as a homogeneous structure, thin and transparent as water. "In all pollen in which the external membrane is altogether smooth, in all those which possess but a single plait, in a great part of those which have three plaits, in those which have spiral plaits, and in a great many of those which are provided with pores, the internal membrane forms a cell altogether spherical or ellipsoidal. On the contrary, in pollen which, like that of the *Onagrariæ*, have a pore at their three truncated angles, or as that of the *Dipsaceæ*, have one upon their three sides, or as among very many species of the *Solaneæ*, *Gentianæ*, *Synantheraceæ*, *Umbelliferæ*, *Apocynaceæ*, *Papilionaceæ*, &c., have one upon their three longitudinal furrows, or as among many species of the *Boraginaceæ*, have a great number, the structure of the internal membrane is not absolutely similar in all its parts; but there exist often, even in the dry granule, papillæ, which are as little blind appendages of the internal membrane. The line of union of these blind appendages with the cell formed by the internal membrane is ordinarily well marked; sometimes, as in the *Onagrariæ*, it presents a thickening, which gives to it the appearance of a white band." I have already explained, that the papillæ, wherever met with, are formed in one of two ways, either, where there are but two membranes, by the protrusion of the internal through fissures or pores in the external, or, where there are more than two membranes, by the protrusion of the one next the external, called by Fritzsche, intextine. When produced in the latter way they are always permanent, that is, they are to be met with in every form and condition of the granule, as they are only in the *Onagrariæ*, and perhaps *Umbelliferæ*, of all the examples of their presence cited by Mohl; but when they are formed in the first way, as they are in all the other instances referred to by Mohl, they are only to be observed where the pollen has undergone either a partial or complete change of form, and are to be regarded as the commencement of pollen tubes just emerging through the fissures in the external membrane, and formed by an elongation or growth of the internal with which they are continuous, without any line of demarcation similar to that described by Mohl. Such therefore is their origin in all cases where there are but two coatings to the pollen granule.

That the external membrane is not continued on to these papillary projections may be seen by an examination of the pollen of *Stachytarpheta mutabilis*, in which there is a distinct line of separation between them and the surface of the external membrane.

With respect to the motion of the "molecular particles" found in the fovilla, Mohl thus expresses himself:—"I cannot refrain from remarking on this subject, that the movement of the grains differs in no way from the motion of all other little organic and inorganic particles; for example, globules of milk, whether vegetable or animal, metallic precipitates, &c.; that their oscillatory motion is altogether the same, and is distinguished in a manner equally striking from the spontaneous movement of infusories."

In concluding my strictures, I would observe, that to Dr. Mohl is due, and ought to be accorded, the highest credit, both for the general accuracy of his observations, as well as for their great extent. Mohl, although in error in a few instances, has been very successful in his perception of the chief differences which characterize the principal types of pollen granule met with in the course of his investigations; and it is a source of no little gratification to me to find that I should have arrived at results in this respect so nearly similar to Mohl's own, deduced from investigations carried on independently of all knowledge of his previous inquiries but that acquired from Lindley's 'Introduction.' Mohl's work in 4to, with 6 plates, was published in Berlin in 1834, a short time subsequently to the appearance of Fritzsche's first memoir in the Transactions of the St. Petersburgh Academy upon the same subject. An abridged translation of Mohl's work is contained in the 'Annales des Sciences Naturelles,' vol. iii. 2nd Series,—Botanique.

Of Mohl's opinions regarding the value of the pollen granule as an assistant in classification, I have spoken fully in a paper, a portion of which is inserted in Annals for last October *.

January 17th, 1842.

XII.—*On* Valerianella olitoria *and* V. gibbosa. By Charles C. Babington, M.A., F.L.S., F.G.S.

In a valuable paper upon the genus *Fedia* (*Valerianella*) published in the 'Linnæan Transactions,' Mr. Woods states that

* The above observations were penned on a perusal of Mohl's work, made some time subsequently to the completion of my paper on the pollen, the greater part of which has yet to appear, and which is delayed until the numerous illustrations which accompany it can be got ready.